Hymenopteran parasitoids and dipteran predators of the invasive aphid *Diuraphis noxia* after enemy introductions: Temporal variation and implication for future aphid invasions

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Abstract

Shifts in prevalence and abundance of hymenopteran parasitoids and dipteran predators, *Diuraphis noxia*, and other aphids were measured in the west-central Great Plains of North America, April–September, in 2001 and 2002, corresponding to over a decade after first detection of *D. noxia* and first release of *D. noxia* enemies. Significant temporal shifts in enemy species prevalence and diversity were detected in this study and more broadly during an 11 year time span. At any given time, some species were relatively common. One parasitoid had been predominant throughout (*Aphelinus albipodus*), two had shifted in dominance (*Lysiphlebus testaceipes* and *Diaeretiella rapae*), three parasitoids had been detected infrequently (*Aphidius avenaphis*, *Aphidius matricariae*, and *Aphelinus asychis*), one parasitoid was detected in the 1990s but not during 2001 and 2002 (*Aphelinus varipes*), two predatory flies occurred at occasional significant levels (*Leucopis gaimarii* and *Eupeodes volucris*), and two parasitoids may have been minor members of the fauna (*Aphidius ervi* and *Praon yakimanum*). Aphid populations detected were usually very low or not detected, precluding estimation of percent parasitism. The best evidence of suppression was observations of parasitoids in the rare case of *D. noxia* exceeding economic thresholds, which complemented past studies using high aphid densities. The *D. noxia* enemies detected were primarily endemic or long-time residents derived from previous introductions. This enemy community may provide flexibility in responding to a future aphid invasion, allowing more strategic use of biological control and other pest management approaches.
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Keywords: *Diuraphis noxia*, *Aphelinus* spp.; Aphelinidae; *Lysiphlebus testaceipes*; *Diaeretiella rapae*; *Aphidius* spp.; Braconidae; *Eupeodes volucris*; Syrphidae; *Leucopis gaimarii*; Chamaemyiidae

1. Introduction

The invasion of *Diuraphis noxia* (Mordvilko) (Homoptera: Aphididae), Russian wheat aphid, into the Great Plains and other areas of western North America occurred rapidly in the late 1980s (Morrison and Peairs, 1998). Within a year following its detection in the west-central Great Plains, Wraight et al. (1993) found two primary parasitoids (Hymenoptera) and unidentified syr-phids and chamaemyiids (Diptera) associated with *D. noxia*. Additional enemies were found in other infested areas (Bernal et al., 1993; Feng et al., 1992; Lajeunesse and Johnson, 1991). Concurrent to the first years of the invasion by *D. noxia* and identification of these enemies, economic damage to wheat and barley due to *D. noxia* was occurring. A decision was made to proceed with a classical biological control effort (Prokrym et al., 1998).

From the late 1980s to mid 1990s greater than 15 million parasitoids and predators derived from exotic collections were released in 16 US states and two Canadian provinces (Prokrym et al., 1998). In the contiguous

wheat production region of the west-central Great Plains (south-eastern Wyoming, south-western Nebraska, and north-central Colorado, USA), releases of hymenopteran parasitoids and dipteran predators were made: three species of Aphelinidae, seven species of Braconidae (Aphidiinae), one species of Chamaemyiidae, and two species of Syrphidae (Brewer and Elliott, 2004). Predatory coccinellids also were released, with no subsequent reports of establishment (Michels et al., 2001; Prokrym et al., 1998).

By the mid 1990s, *D. noxia* infestations had decreased substantially in the west-central Great Plains (Brewer et al., 2001). During this period weather conditions were often conducive to *D. noxia* outbreaks (Legg and Brewer, 1995), and plant cultivars grown were largely susceptible (Souza, 1998). Therefore, it was appealing to attribute *D. noxia* population declines, in good part, to the released biological control agents. *Aphelinus albipodus* Hayat and Fatima (Hymenoptera: Aphelinidae) and *Diaeretiella rapae* (M'Intosh) (Hymenoptera: Braconidae, Aphidiinae) were widespread in the region after release of the exotic *A. albipodus* and exotic strains of *D. rapae* (Brewer et al., 2001), and *A. albipodus* had suppressed *D. noxia* population growth in replicated field tests (Brewer et al., 1999). But it was most likely that exotics introduced for *D. noxia* control, long-time residents established from previous introductions, and endemic species were all represented in enemy collections obtained 3–16 years after *D. noxia*'s invasion (Brewer et al., 2001; Noma et al., 2005). Sometimes distinctions of the source of the collected specimens, exotic or pre-existing resident, could not be made because some released exotic strains were indistinguishable from resident populations of the same species. The time period of enemy response and confusion of source of enemies complicate speculation on the status of *D. noxia* enemies. Demographic information on species occurrence and abundance may help address these issues and the broader issue on how to respond to future aphid invasions.

Here, we expand upon the work of Noma et al. (2005), presenting seasonal shifts in prevalence and abundance of parasitoids and dipteran predators, *D. noxia*, and other aphids, corresponding to 15–16 years after first detection of *D. noxia*, 12–13 years after the first release of *D. noxia* enemies, and 5–6 years after their last release in the west-central Great Plains. We discuss the relevance of these data and prior data from the same region accumulated over a decade (Ahern and Brewer, 2002; Brewer et al., 2001; Wraight et al., 1993) in considering how to address future aphid invasions.

2. Materials and methods

2.1. Farm sites

Primary parasitoids and predatory flies were collected in 2001 and 2002 at 16 farm sites scattered throughout a 14,000 km² region of contiguous wheat production in the west-central Great Plains. Secondary parasitoids also were collected, but we focused on primary parasitoids due to low recovery of secondary parasitoids using our detection method (<1% of specimens collected), and difficulties in their identification. The farm sites were characterized by high elevation (1280–1830 m above sea level), temperature, and rainfall averages conducive to *D. noxia* outbreaks (Legg and Brewer, 1995), planting of *D. noxia*-susceptible wheat, *Triticum aestivum* L. (Souza, 1998), and dryland farming focused on winter wheat production (Peterson et al., 1996).

Each farm site consisted of a cropping area and an adjacent grassland area. The cropping area was a spatial sequence of alternating crop and fallow strips, 30–160 m wide and 0.25 to several kilometers in length. The crop strips were winter wheat, and some growers planted strip additions of a spring crop in rotation with the wheat and fallow strips. The most common spring crop sown was sunflower, *Helianthus annuus* L., with rare substitutions of oats, *Avena sativa* L., and proso millet, *Panicum miliaceum* L., depending upon soil moisture considerations. Insecticides had not been used during the previous five years except for sunflower pest control. The adjacent grasslands were managed grasslands (for grazing or conservation) of the more northern extensions of the shortgrass prairie (Simms, 1988).

2.2. Collection procedures

At each farm site, *D. noxia*-infested wheat was exposed to ovipositing parasitoids and predatory flies, and resulting progeny were reared in the laboratory to the adult stage and identified (Milne, 1995). This procedure allowed sampling where *D. noxia* populations in wheat had been commonly low (i.e., <1% of tillers infested) compared with populations often exceeding an economic threshold of 10% infested tillers from the late 1980s to the mid-1990s (Brewer et al., 2001). The method also assured that species collected were able to complete development on *D. noxia*.

Preparation and field exposure of *D. noxia*-infested wheat was fully described by Noma et al. (2005). Briefly, the winter wheat cultivar 'Buckskin' was planted in pots, which were infested with laboratory-maintained *D. noxia*. A large number of aphids averaging over 300 per pot assured ample supply of aphids for consumption by predatory fly larvae without depletion of aphids for parasitism (parasitism did not exceed 10%). At each farm site, eight pots were placed within grassland and 22 within crop strips along two line transects. The transects stretched up to 400 m into a field across the first three crop strips, always including at least one wheat and fallow strip and one alternate crop strip if present at a site. A transect extended the opposite direction up to 150 m into the adjacent grassland.

To maximize the chance of capturing aphid enemies, the pots were left in the field as many days as possible, 2–7 days, but before plant wilting was anticipated to occur. Collections were taken five times each year between late April and late September. After exposure to enemies, all pots were transported to the greenhouse, covered with organdy fabric, and incubated for about 1 week. The plants were cut and placed in emergence canisters to capture emerging parasitoids and predatory flies. They were examined under a dissection microscope for species identification using keys principally from Vockeroth (1992), Pike et al. (1997), and Tanasijtshuk (1996). Identifications of subsets of the collections were verified by specialists (see Acknowledgements). To check for possible contamination by parasitism in the greenhouse, four extra pots were left in the greenhouse during each collection period.

During each farm site visit to set out pots, aphid densities in crop strips were estimated by visual inspection of randomly selected tillers of wheat ($n = 100$) and sunflower plants ($n = 60$). Aphids were identified using pictorial keys (Halbert et al., 1988). The proportion of wheat tillers infested with *D. noxia*, number of other aphid species per wheat tiller, and number of *A. helianthi* per sunflower plant were recorded. Notes on crop phenology also were taken. For the grasslands, aphid observations were limited to plant inspection in the area where pots were placed in the field. Wheatgrasses in grasslands are hosts of *D. noxia*, although relatively minor field hosts compared with wheat (Brewer et al., 2000).

2.3. Data analyses

The analyses were chosen to differentiate among enemy species in their prevalence and abundance through the growing season, and to determine whether enemy abundance was associated with aphid abundance. The cropping structure and composition of the surrounding landscape will be considered elsewhere for key species identified. For each collection period and enemy species, mean detection frequency (number of pots with an enemy species detected divided by total number of pots), and mean abundance (number of an enemy species in the pots divided by the total number of pots) were calculated for each of the 16 farm sites. The multivariate Hotelling T^2 test was used to test for equality of detection frequencies and abundance among the enemy species for each collection period, followed by pair-wise mean comparisons at $\alpha = 0.05$ (Proc Anova, Manova statement; Littell et al., 1991). For each enemy species and year of the study, correlation analysis (Proc Corr; SAS Institute, 2000) was used to compare the mean detection frequencies with corresponding mean abundance at the 16 farm sites for all collection periods.

Aphid abundance in wheat (mean proportion of *D. noxia*-infested tillers and mean number of other cereal aphids per tiller) and sunflower (mean *A. helianthi* per plant) at each farm site and an overall mean across farm sites was calculated for each species detected during each collection period. Aphid abundance data of the three kinds collected were considered as an explanatory variable of enemy abundance for each species using regression analysis across all collection periods and farm sites for each year (Proc Reg; Littell et al., 1991). The analyses were redone comparing enemy abundance of the second to fifth collection periods to aphid abundance estimated from the previous collection periods about 1 month earlier.

3. Results

3.1. Enemies detected

Eight parasitoid and two predatory fly species were detected: *A. albipodus* (Hymenoptera: Aphelinidae), *Lysiphlebus testaceipes* (Cresson), *Aphidius avenaphis* (Fitch), *Aphidius matricariae* Haliday (Hymenoptera: Braconidae, Aphidiinae), *Leucopis gaimarii* Tanasijtshuk (Diptera: Chamaemyiidae), and *Eupeodes volucris* Osten Sacken (Diptera: Syrphidae) (Figs. 1 and 2). Collected, but not shown and not included in analyses, were *Aphelinus asychis* (Hymenoptera: Aphelinidae), *Aphidius ervi* Haliday, *D. rapae*, and *Praon yakimanum* Pike & Starý (Hymenoptera: Braconidae, Aphidiinae), because they were rarely detected (no more than 0.6% of the pots) and their abundance was low (did not exceed an average of 0.05 parasitoids per pot, except one instance when *A. asychis* averaged 0.25 parasitoids per pot in August 2001). Noma et al. (2005) reported species records and geographic range of the species not presented here. Coccinellids were rarely detected in the field or in the aphid-infested potted plants. In analysis of data of the six enemy species presented here, significant differences in detection frequency and abundance were seen among the species during each collection period of the 2 years ($P < 0.05$ in all Hotelling T^2 tests).

3.2. Enemy seasonal occurrence and abundance

Major shifts in rank order of detection frequency of the enemies were seen across the 5 months of collections each year. *A. albipodus* was the most frequently occurring of the parasitoids in three of five collections in 2001, and the most frequently occurring of all enemies detected late season in August and September, 2001 (Fig. 1A). This is in contrast to 2002 when *A. albipodus* was more frequent in early collections through July (Fig. 2A). *L. testaceipes* occurred sporadically in 2001 (Fig. 1A), but in 2002 it was similar to or exceeded levels of *A. albipodus* late season during the last two collections (Fig. 2A). *A. avenaphis* and *A. matricariae* were detected in about 2.5% of the pots during the late April collection in 2002 but were otherwise rarely detected (Figs. 1A and 2A).
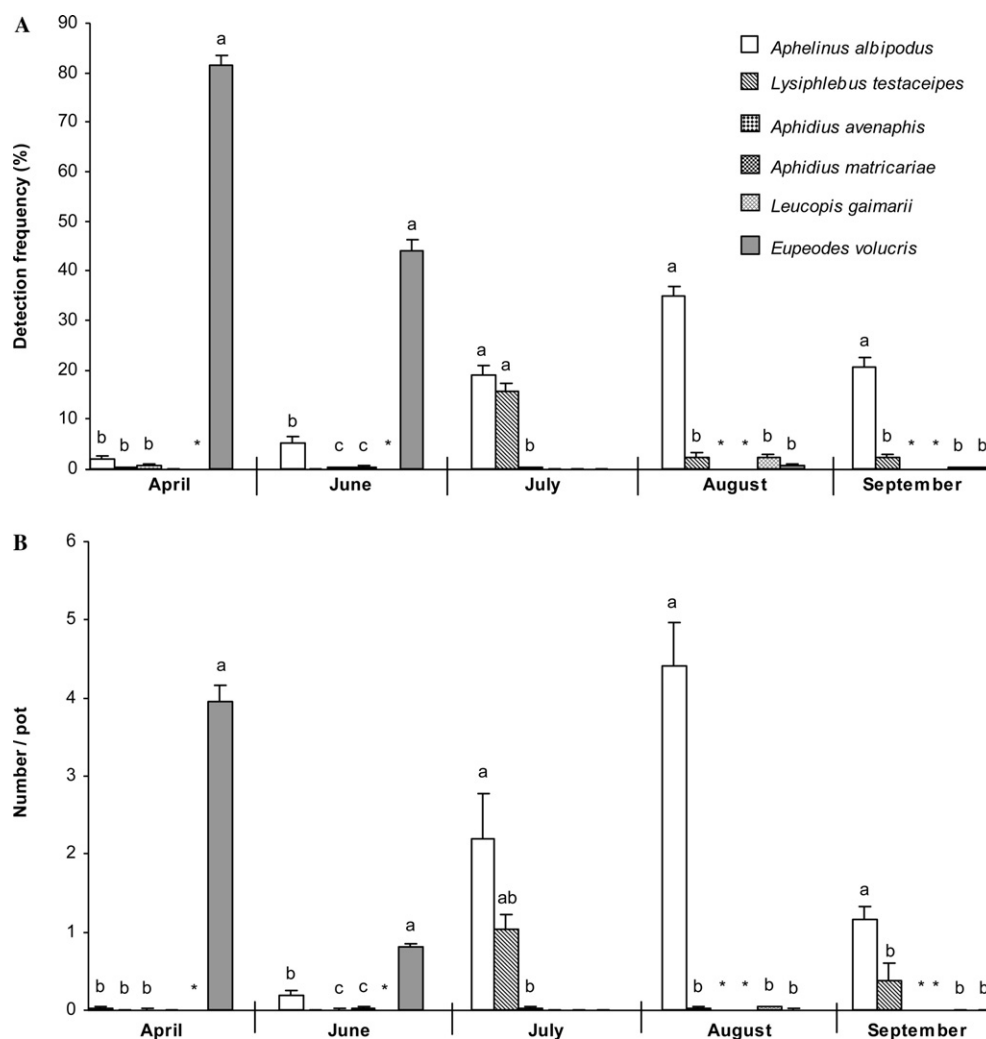
Fig. 1. Detection frequencies (A) and abundance (B) of *D. noxia* enemies collected from exposed *D. noxia*-infested plant material placed at farm sites in the west-central Great Plains, 2001. A star indicates no estimate available, because the species was not recognized at the time of collection (*L. gaimarii*) or a greenhouse contamination precluded use of the data (*Aphidius* sp.). For each month, different letters above the bars indicate significant mean separation, pair-wise comparisons of the Hotelling T^2 test. Lines attached to the bars are SEMs.

Two dipteran predators, *E. volucris* and *L. gaimarii*, were prevalent in collections when detected. *E. volucris* was frequently detected in 2001 through June (Fig. 1A). The syrphid was rarely detected the rest of the 2001 and throughout 2002 (Figs. 1A and 2A). *L. gaimarii* occurred frequently (about 50% of the pots) during the first two collections in 2001, as supported by laboratory notes. The specific frequency of occurrence was not recorded because this species was not identified as an aphid predator until the third collection. During 2002, it was detected through the July collection periods (Fig. 2A). There was very similar discrimination among the species using the frequency and abundance means (Fig. 1A compared with Fig. 1B, Fig. 2A compared with Fig. 2B), as substantiated by strong positive frequency—abundance correlations ($r > 0.75$ and $P < 0.0001$ for nine correlation tests, and $r = 0.50$ and $P = 0.0004$ for one test).

3.3. Enemy associations with aphids

In both years of the study, wheat was harvested by mid-July and emergence of the fall planting occurred in September before the last collection period. The spring sown grains and grasslands were growing in July and August when wheat was not in cultivation. Aphid species collected from wheat were *D. noxia*, *Rhopalosiphum maidis* (Fitch) (corn leaf aphid), *Rhopalosiphum padi* L. (bird cherry—oat aphid), and *Schizaphis graminum* (Rondani) (greenbug). On sunflower, only *Aphis helianthi* Monell was collected. In 2001, all aphids in wheat were rarely detected and only after the emergence of new wheat in September, while *A. helianthi* on sunflower reached an average of 12 aphids per plant by late September (Table 1). In 2002, *D. noxia* was more common (Table 1), exceeding an economic level of 10% infested tillers in one field by early June. As in 2001, other cereal
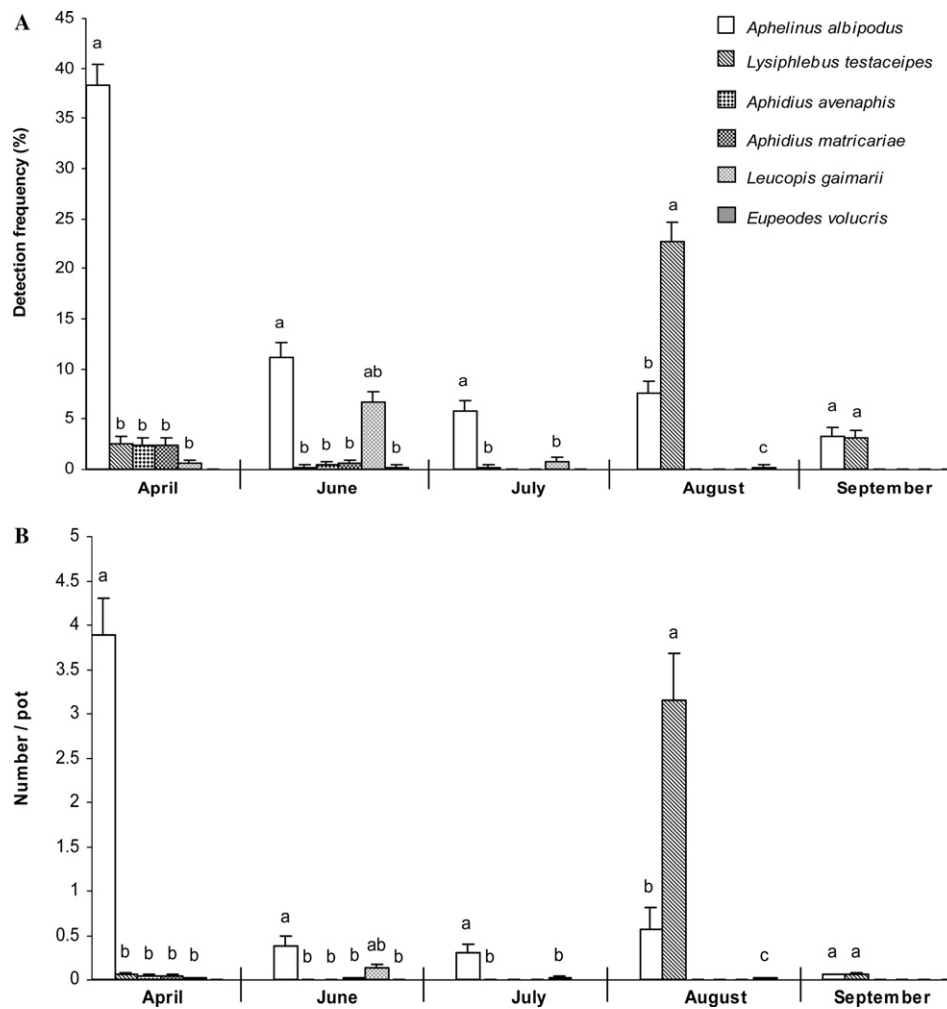
Fig. 2. Detection frequencies (A) and abundance (B) of *D. noxia* enemies collected from exposed *D. noxia*-infested plant material placed at farm sites in the west-central Great Plains, 2002. For each month, different letters above the bars indicate significant mean separation, pair-wise comparisons of the Hotelling T^2 test. Lines attached to the bars are SEMs.

Table 1
Aphids on Wheat and Sunflower Collected from Farm Sites in the West-Central Great Plains, 2001 and 2002

Date	N	Crop phenology[a]		Wheat[b]				Sunflower[c]
		Wheat	Sunflower	*D. noxia*	*R. maidis*	*R. padi*	*S. graminum*	*A. helianthi*
2001								
April 24	14	Tillering	Not emerged	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
May 29	13	Booting	Not emerged	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
August 5	16	Harvested	V stages	–	–	–	–	0.41 (0.12)
August 28	15	Harvested	R-2 to 4	–	–	–	–	1.80 (0.83)
September 29	14	Seedling	R-7 to 8	0.009 (0.009)	0.02 (0.008)	0.05 (0.03)	0.06 (0.05)	12.12 (11.26)
2002								
April 25	14	Tillering	Not emerged	0.007 (0.007)	0 (0)	0 (0)	0 (0)	–
June 5	15	Booting	Not emerged	0.04 (0.02)	0 (0)	0 (0)	0 (0)	–
July 14	16	Ripening/harvested	R-2 to 3	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
August 18	14	Harvested	R-5	–	–	–	–	0.07 (0.05)
September 25	15	Seedling	R-7 t0 8	0 (0)	0.002 (0.002)	0.005 (0.002)	0.0008 (0.0008)	0.004 (0.004)

Missing data occurs when the crop is not in cultivation at time of sampling.
[a] Wheat terminology (Zadoks et al., 1974); sunflower terminology, V = vegetative and R = reproductive (Schneiter and Miller, 1981).
[b] *D. noxia*: mean (SEM) proportion of 100 tillers infested. *R. maidis*, *R. padi*, and *S. graminum*: mean aphids per tiller (SEM) of 100 tillers sampled per farm site.
[c] *A. helianthi*: mean aphids per plant (SEM) of 60 plants inspected per farm site.

aphids were sporadic and not detected until after emergence of fall-planted wheat. *A. helianthi* was detected sporadically on sunflower in 2002 (Table 1). No aphids were observed in the grasslands during our visual inspections.

Analyzing the association of enemies with aphids, only 27 linear associations of enemies and aphids taken from the same collection period were tested because aphid data were at times unavailable (Table 1). None of the linear trends were significant ($P \geqslant 0.10$). Comparing enemy abundance of the second to fifth collection periods to aphid abundance from the previous collection periods allowed for 11 linear tests. All were not significant ($P \geqslant 0.10$) when a few outlying data points were excluded that were associated with one field where *D. noxia* populations exceeded 10% infested tillers.

4. Discussion

4.1. Status of parasitoid and predatory fly enemies of D. noxia

Aphelinus albipodus and *L. testaceipes* were the predominant members of the enemy fauna, occurring in significant numbers at some part of the season, 2001 and 2002. *A. albipodus* has been a dominant member of the *D. noxia* enemy fauna for an 11 year observation period (Figs. 1 and 2, Ahern and Brewer, 2002; Brewer et al., 2001); whereas, *L. testaceipes* through most of the 1990s was detected parasitizing *D. noxia* at much reduced levels (Brewer et al., 2001; Burd et al., 2001). The predatory fly *L. gaimarii* was an occasionally dominant member of the fauna during the course of this study. Its inconspicuous nature, difficulties in collecting it, and only recent recognition (Tanasijtshuk, 1996) may have resulted in previous under-reporting, including in our work the first year. The other predatory fly, *E. volucris*, was a significant member of the fauna when it occurred (Fig. 1). Two other members of the enemy fauna were detected at much lower levels (*A. matricariae* and *A. avenaphis*) (Figs. 1 and 2). *A. matricariae* was previously found in low numbers, and *A. avenaphis* was not previously detected in our study region (Brewer et al., 2001). *D. rapae*, *A. asychis*, and *A. varipes* also were included in the fauna list for a total of seven parasitoid species. Although detected at trace levels (*D. rapae* and *A. asychis*) or not detected (*A. varipes*) in 2001 and 2002, they had been detected at more substantial levels coincident to higher populations of *D. noxia* (Brewer et al., 2001; Burd et al., 2001). *P. yakimanum* and *A. ervi* may be minor members of the fauna, which would expand the parasitoid fauna list in the west-central Great Plains to nine species. *Praon* sp. and *A. ervi* had been detected parasitizing *D. noxia* at trace levels over a decade of observation in the region (Brewer et al., 2001; Noma et al., 2005).

In surveys early in *D. noxia*'s invasion of our study region and before release of biological control agents, Wraight et al. (1993) detected a fairly diverse set of enemies in low numbers, representing aphelinids, braconids, chamaemyiids, and syrphids. About the same time period, Lajeunesse and Johnson (1991) reported aphelinids, chamaemyiids, syrphids, and other predators north of our study region. Some indistinguishable introduced and endemic strains present confusion on the origin of current detections, most importantly *D. rapae* (Burd et al., 2001). Also, Noma et al. (2005) reported *A. albipodus* as derived from exotic introductions, but *A. albipodus* may represent a complex of cryptic species (J. Woolley, pers. comm.), some of which likely predated the introductions. With these possible exceptions, the gradual increase in detections over this 11 year window and the early detection of a fairly diverse enemy fauna are most consistent with gradual adaptation of pre-existing species to an invading species as prey (Cornell and Hawkins, 1993). The evidence is most consistent with the assertion that parasitoids and predatory flies of *D. noxia* in the west-central Great Plains are primarily endemic species or long-time residents derived from previous introductions.

4.2. Regional comparisons and factors associated with enemy species variation

There is now a substantial enemy fauna associated with *D. noxia* in the west-central Great Plains. Primary parasitoid species found in the west-central Great Plains (four braconids in three genera and three aphelinids, and possibly two other braconids) were similar in number and diversity to the *D. noxia* parasitoid fauna reported from Washington state (eight braconids in four genera and three aphelinids: *L. testaceipes*, *A. avenaphis*, *A. matricariae*, *A. ervi*, *D. rapae*, *P. yakimanum*, *Praon unicum* Smith, *Praon occidentale* Baker, *A. albipodus*, *A.varipes*, and *A. asychis* [Pike et al., 1997, 2000]). The west-central Great Plains fauna represents one additional parasitoid family when compared with the fauna reported from the Czech Republic (eight braconids in four genera: *Aphidius colemani* Viereck, *A. matricariae*, *A. ervi*, *Aphidius rhopalosiphi* DeStefani, *Aphidius picipes* (Ness), *D. rapae*, *Praon volucre* (Haliday), and *Ephedrus plagiator* (Ness) [Starý, 1999]). In Britain where *D. noxia* does not occur, the cereal aphid parasitoid fauna is represented principally by six braconids in four genera (*A. ervi*, *A. rhopalosiphi*, *A. picipes*, *P. volucre*, *E. plagiator*, and *Toxares deltiger* (Haliday)) with additional minor species (Wratten and Powell, 1991).

We saw significant year-to-year and farm-to-farm shifts. *L. testaceipes* was the most significant braconid in 2001 and 2002, while *D. rapae* played this role in the early to mid 1990s when *D. noxia* was more abundant (Brewer et al., 2001). Parasitoid species shifts in

prevalence from year-to-year have been documented in Britain cereal fields (Wratten and Powell, 1991). Noma et al. (2005) reported variation of enemy occurrence across the 16 farm sites of our study region, similar to the farm-to-farm variation reported in Britain (Wratten and Powell, 1991). The striking feature was the high temporal and farm-to-farm variation in species prevalence and abundance, with one or a few species typically common during any one of collection periods (Figs. 1 and 2).

4.3. Diuraphis noxia suppression

Low aphid densities precluded an estimation of field percent parasitism and detection of relationships between parasitoid abundance and aphid abundance. The best evidence of *D. noxia* suppression was field observations of parasitoids in the rare instance of *D. noxia* population exceeding economic thresholds. *D. noxia* mummies of the aphelinid-type (black cigar-shaped mummies) were readily detected in early June, 2002, when *D. noxia* populations in one field exceeded 10% infested tillers at about the boot stage of wheat development. Coinciding with plant senescence, *D. noxia* and mummies were not observed by the next collection period, but *A. albipodus* adults were still readily detected (Fig. 2). At other collection periods mummies were not detected, aphid populations were very low (Table 1), but adult parasitoids were detected parasitizing *D. noxia* on our potted plants placed in the field (Figs. 1 and 2). This same pattern was seen in *A. albipodus* response to high *D. noxia* densities in replicated field tests (Brewer et al., 1999). For winter wheat of western North America, *D. noxia* may occur on fall-sown wheat, overwinter on wheat, and reproduce on the same wheat crop the following spring (Elliott et al., 1998). Some members of the enemy community were active throughout the season (Figs. 1 and 2). Variation in parasitoid activity in time (seasonally and year-to-year) and space (farm-to-farm) has been well recognized as relevant to aphid regulation (Wratten and Powell, 1991). They observed that roles of individual cereal aphid parasitoids were variable year-to-year and farm-to-farm, but the enemy community was sufficiently large to often contribute to aphid suppression.

Michels et al. (2001) found native coccinellids had much more impact on *D. noxia* than parasitoids in the southern region of the Great Plains. Our work in 2001 and 2002 was relevant to low-density aphid populations; whereas, Michels et al. (2001) reported from areas of higher *D. noxia* populations on wheat. Densities commonly ranged from 10 to 100 aphids per tiller in April and May. During earlier work in our study area when aphid densities were higher, coccinellids were more commonly encountered, although none of the species detected originated from introductions for *D. noxia* control (Prokrym et al., 1998). Density sensitivity may be important for some of the parasitoids we detected. Up to

the mid 1990s, another species (*D. rapae*) was more prevalent coinciding with higher *D. noxia* populations (Brewer et al., 2001), while *A. albipodus* was dominant during high *D. noxia* population levels (Brewer et al., 2001) and remained dominant during current low-density aphid populations (Figs. 1 and 2). Overall, the current *D. noxia* enemy fauna in the west-central Great Plains appears to be maintaining itself at low levels in a low-aphid density environment, with occasional significant detections of two parasitoids and two predatory flies. The species diversity of the *D. noxia* enemy fauna and variation in seasonal and decade-long prevalence are consistent with the view that species richness is beneficial to biological control (Cornell and Hawkins, 1993).

4.4. Future aphid invasions

With a future aphid invasion in the cereal-based agroecosystem of the west-central Great Plains, this enemy community may provide the needed flexibility to respond to a new invader. In fairness, political pressures may be intense during early stages of an invasion that causes economic harm, leading to an argument for quick action to introduce biological control agents (Ehler, 2000), as occurred in response to the invasion of *D. noxia* (Prokrym et al., 1998). Enemy assessments early in the invasion phase may detect a fairly diverse enemy fauna (Wraight et al., 1993) but underestimate eventual effect of pre-existing enemies that adapt to use of the invading aphid as prey. Other emerging public interest concerns, such as non-target effects of enemy introductions, also are relevant to planning strategies for management of invasive species (Ehler, 2000).

Of the *D. noxia* enemies detected in the west-central Great Plains, one parasitoid had been predominant through our 11 year observation (*A. albipodus*), two had shifted in dominance (*L. testaceipes* and *D. rapae*), three parasitoids had been detected infrequently (*A. avenaphis*, *A. matricariae*, and *A. asychis*), one parasitoid was not found in our work but was detected in the 1990s (*A. varipes*), two predatory flies occurred at occasional significant levels (*L. gaimarii* and *E. volucris*), and two parasitoids may have been minor members of the fauna (*A. ervi* and *P. yakimanum*). *D. noxia* enemies in the west-central Great Plains appear to be primarily endemic species or long-time residents derived from previous introductions. In response to future aphid invasions into this system, we see merit in study of the existing enemy fauna and enemy–aphid–plant interactions even if enemy surveys soon after first detection of the invading aphid report no significant impact on the aphid. Adaptation to the new prey may occur in time. The study of the existing enemy fauna in conjunction with the foreign exploration phase of the classical biological control approach may provide the best opportunity to employ strategic use of conservation biological control and other pest management approaches

and selected release of classical biological control agents in response to a future aphid invasion.

Acknowledgments

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